



The taxonomy of the Asian Wild Buffalo from the Asian mainland

By C. P. GROVES

Department of Archaeology and Anthropology, Australian National University, Canberra, Australia

Receipt of Ms. 01. 11.1995

Acceptance of Ms. 23. 01. 1996

Abstract

Examined were skulls and horns of wild buffalo (*Bubalus arnee*) from India and Southeast Asia. Three subspecies are clearly distinguishable: one from Assam, one from Nepal and Central India, and one from Thailand and Cambodia. Several names are available; their type specimens had been lost or misidentified, but were discovered in this study, and allocated to one or other of the two Indo-Nepalese taxa. A new subspecies is described for the Thailand and Cambodian population.

Introduction

Wild buffalo (*Bubalus*) in Asia are known from India and Nepal, Sri Lanka, Burma, Thailand, Cambodia, Vietnam, Malaysia (Sarawak), Indonesia (Sumatra, Java, Sulawesi), and the Philippines (Mindoro). Those from Sulawesi are assigned a separate subgenus, *Anoa*, and those from Mindoro, while referable to the nominotypical subgenus, are regarded as belonging to a unique species, *Bubalus mindorensis* (see GROVES 1969). All others belong to the same species as the domestic buffalo, *Bubalus bubalis* (Linnaeus, 1758).

THOMAS (1911) found that LINNAEUS'S (1758) description of *Bos bubalis* refers to the domestic buffalo, and fixed the type locality as "Italy (Rome)". LINNAEUS'S (1758) brief descriptive notes make it clear that he had domestic buffaloes in mind.

Whether wild species should be referred to by names first given to domestic forms is a controversial matter, and has been most recently been discussed by GROVES (1995 a), who refers to domestic forms as "parataxa", rather than true taxa; as such, it can be maintained that they have no place in biological nomenclature. Pending a new consensus on the question, in this study, names given to domestic buffalo will be ignored; the prior available name for a wild buffalo is *Bubalus arnee* (Kerr, 1792).

The former and present distribution of Asian wild buffalo is carefully reviewed by HEDGES (1995). The species is today in danger of extinction as a wild animal. On the Asian mainland it still exists in the following pockets of population (A. CHOUDHURY, H. K. DIVEKAR, J. HEINEN, T. PRAYURASUDHI, SUN HEAN, LE VU KHOI, pers. comm.): Assam and adjacent states, and Bhutan (several reserves); Bastar and Raipur districts, Madhya Pradesh (four reserves); Nepal (Kosi Tappu National Forest); Thailand (Huai Kha Khaeng Wildlife Sanctuary); scattered populations on the Cambodia-Vietnam border. Of these the only reasonably substantial population, numbering some 3300–3500, is that centred on Assam (CHOUDHURY 1994). In 1979, an undoubted wild buffalo turned up in the Panna district, far from its known present-day distribution (HASAN 1980). As later pointed out (ARUN SINGH 1980), this distance, about 225 km northwest of the species' nearest present occurrence in Raipur district, is well within the known seasonal ranging distance of buffaloes in the last century.

Feralized buffalo (domestic stock run wild) have established themselves in many places. In most cases there should be little problem in distinguishing them from true wild buffalo; this is especially the case in peninsular India and Pakistan, where the domestic buffalo are "River" breeds, quite different in appearance from wild buffalo. River buffaloes have from time to time been exported to Southeast Asia, and even run wild; the type specimen of so-called *Bubalus moellendorffi* Nehring, 1894 (ZMB 14803), from Busuanga in the Philippines, is a feral river buffalo. In the case of "Swamp" Buffalo, the much less highly bred domestic buffaloes of Southeast Asia, there would be more of a problem; a specimen from the Upper Chindwin (BM 17.7.8.3) is very small and short-horned compared to specimens from Assam, Chittagong and Pegu, and assorts in all analyses with domestic swamp buffalo, but no such criteria can be applied in the case of the insular populations (see above), and it is still an open question whether any are genuinely wild, rather than feral (HEDGES 1995). For the moment, it should be noted that the insular buffaloes are much smaller, and have very much shorter horns, than those from the mainland. The cranial capacity criterion (HERRE and RÖHRS 1990) could presumably be applied; the true status of the wild-living buffalo of Sri Lanka and Southeast Asia will be the subject of future investigations.

There is also the problem of interbreeding between wild buffalo and local domesticates. For the moment, let it be said that with one exception, which will be discussed below, all specimens of mainland wild buffalo which I have been able to study (mostly collected before the middle of this century) are sharply distinct from domestic buffalo of whatever breed.

Finally, the interrelationships of the mainland groups of wild buffalo are in need of revision: are there subspecies; if so, how many? This problem, a rather crucial one for conservation, is the subject of the present study.

Materials and methods

Skulls and horns of wild buffaloes were studied in the following collections (with their abbreviations): Natural History Museum, London (BM); Powell-Cotton Museum, Birchington, Kent (PC); Royal Scottish Museum, Edinburgh (RSM); National Museum of Natural History, Paris (MNHN); Natural History Museum, Marseille (MAR); Zoological Museum, Hamburg (ZMH); Zoological Museum, Berlin (ZMB); University Zoological Museum, Copenhagen (CPH); Natural History Museum, Florence (FIR); Royal Natural History Museum, Stockholm (RMS); Indian Museum (IM) and Zoological Survey of India (ZSIC), Calcutta; Zoological Survey of India, Madras (ZSIM); Indian Forestry College, Dehra Dun (IFC); National Zoological Reference Collection, Bangkok (NRC); private collection of VAN INGEN and VAN INGEN Taxidermy, Mysore (VI); private collection of Maharana of Wankaner, Gujarat (WAN); private collection of Maharaja of Jaipur (JAI); and private collection of CHOKCHAI BULUKUL, Bangkok (CHOK) (Tab. 2).

The following skull and horn measurements (in mm) were taken on each specimen, if complete enough (some were frontlets and horns or stuffed heads and horns only), and if fully accessible for measurement (some were hung on walls and could not be moved): (1) GSL: Greatest Skull Length (ends of premaxillae to back of occiput); (2) BB: Biorbital Breadth (across lower margins of orbits); (3) PB: Postorbital Breadth (least width of forehead behind orbits); (4) OBG: Occipital Breadth Greatest (in mastoid region); (5) OBL: Occipital Breadth Least (at constriction between horn bases and mastoids); (6) BHB: Breadth Between Horn Bases (least distance across forehead between horn cores); (7) PBN: Posterior Breadth of Nasals (across nasals, at widest part at suture with frontal); (8) ABN: Anterior Breadth of Nasals (across nasals, at widest part at premaxillary sutures); (9) NL: Nasal Length (greatest length along internasal suture); (10) BL: Basal Length (ends of premaxillae to basion); (11) MT: Maxillary tooththrow length; (12) TT: Tip-to-Tip (distance between tips of horns); (13) BT: Base-to-Tip (distance between a horn tip and nearest point of base on same side); (14) SP: Span (greatest distance across lateral surfaces of horns); (15) BD: Basal Diameter (greatest diameter of one horn at base); (16) BO: Base-to-Outer (from a horn base to most distant point of curve on same side). Note that all horn measurements were taken on the sheath, not the core.

The specimens were divided according to region: Assam, "Upper India" (meaning Nepal; from the Hodgson collection of the Natural History Museum, London); "Central India", Thailand, and Cambodia. There were also individual specimens from the Chittagong Hills; the Sunderbans; Upper Chindwin; Pegu; and Song R., Lagna, S. Vietnam, which were considered separately, as was an unlocalised skull from the RSM which was identified as the type specimen of *Bos arnee* Kerr (see below). The different regions, and individuals, were compared by univariate (t-tests and coefficient of difference) and multivariate methods, the latter using SPSS Discriminant on the Durras Mainframe at the Australian National University. Three Discriminant Analyses were run: (1) all cranial measurements (nos. 1–10); (2) all horn measurements (nos. 12–15); and (3) a combination of skull (nos. 1–3, 5, 7–9) and horn (12–14, 16) measurements, designed to maximise the number of available specimens. After initial runs, "Upper India" and "Central India" were combined as "C/U.India", as was Thailand with Cambodia: despite the small sample sizes, no clear discrimination emerged between them. The analyses were thereafter based on three samples (Assam; C/U India, and Thai/Cambodia), with Chittagong, Sunderbans, Upper Chindwin, Pegu, Vietnam and the presumed type of *arnee* entered as unknowns.

Results

Sexing

Rather few skulls (25 in all) are sexed; those that are show a good average difference in the diameter of their horns at the base. In the Assam and C/U.India samples, Basal Diameter is 138–185 (mean 166.11) mm in 9 males, 114–158 (mean 129.38) mm in 8 females; in Thai/Cambodia, 136–163 (mean 148.33) in 3 males, 100–133 (mean 118.67) in 3 females.

Table 1. Comparative skull and horn variables for mainland wild buffalo (in mm) (SD = standard deviation; n = number)

	Assam	C/U.India	Thai/Cambodia
Geatest skull length (GSL)	594.7	561.5	547.9
SD	22.8	15.2	13.7
n	26	11	14
Biorbital breadth (BB)	253.5	239.4	233.3
SD	13.2	10.5	10.1
n	27	11	16
Upper tooththrow length (MT)	159.8	160.4	142.5
SD	7.7	7.5	10.3
n	21	11	6
MT as % GSL	26.9	28.2	25.8
SD	1.4	1.1	1.5
n	21	11	6
Horn span (SP)	1 313.4	1 141.5	1 442.7
SD	327.4	220.8	324.9
n	28	15	16
SP as % GSL	224.1	192.6	256.1
SD	50.8	26.3	87.2
n	26	11	14
TT as % SP	62.5	56.5	81.3
s. d.	14.7	18.1	9.7
n	28	15	8

Table 2. List of specimens and localities (for abbreviations of collections, see text)

Assam		
"Assam"		BM 41.73, 84.1.22.4, 1938.7.1.1, Acton unreg.; KOL; CPH 288; IFC; VI; ZSIC unreg. (3); NRS unreg.; WAN; ZMB 37377
Mishmi Hills	28.00 N 96.00 E	BM 91.8.7.215 (type <i>fulvus</i>)
Sadiya	27.49 N 95.38 E	Bentham 10 (?paratype <i>fulvus</i>)
Dhubri	26.01 N 90.00 E	BM 20.5.14.1, 12.10.31.84, 91.8.7.213
Bansbaree (= Palnsbari)	26.07 N 91.30 E	FIR 8070, -1
Tezpur	26.38 N 92.49 E	BM 55.1.10.1
Mikir Hills	26.30 N 93.00 E	ZMH 384
Gola Ghat	26.30 N 93.59 E	BM 44.129, -130
Guwahati	26.10 N 91.45 E	BM 12.10.31.83
Kaziranga	26.50 N 93.30 E	FRI
Kuch Behar	26.18 N 89.32 E	BM 5.7.29.1; JAI
Faridpur	23.29 N 91.45 E	ZSIC unreg.
Chittagong Hills	22-23 N 92-92.30 E	BM 30.10.5.1
Central and "Upper" India		
"North from Bengal"		?RSM (?type <i>arnee</i>)
Ganjam	19.28 N 85.05 E	FRIM unreg.
Raipur	21.16 N 81.42 E	BM unreg.
"Upper India" (= Nepal)		BM 45.1.8.142, -3
Nepal		BM 59.471
"Central India"		BM 41.172
Junga	20.08 N 82.17 E	PC C.P.6
Gomrapodor	19.57 N 82.23 E	PC C.P.12
Torenga	20.11 N 82.20 E	PC C.P.10
Indgaon	20.05 N 82.26 E	PC C.P.5, -7
Purneah	25.47 N 87.28 E	BM 91.8.7.214
Sunderbans	22-23 N 88-91 E	PC Sund.5
Kukri-Mukri	?southwestern Sunderbans	type <i>septentrionalis</i> (not seen)
Thailand, Cambodia, Burma, Vietnam		
Pegu	17.18 N 96.31 E	BM 26.9.5.2
Kokan, E. Siam (? = Khon Kaen, 16.25 N 102.40 E)		CPH unreg.
Mae Wong, Nakhon Sawan	15.41 N 100.07	NRG unreg.
Thailand		CHOK (7)
"Siam"		CPH 71, 1262, 1263
Cambodia		NRC unreg.; MAR 122, 138
Langna, Song River	11.00 N 107.20 E	MNHN 1932

Between males and females, for India $t = 4.559$ at 15 d.f., $p < 0.001$; for S.E. Asia, $t = 2.363$ at 4 d.f., $p < 0.1 > 0.05$. I attempted to sex other skulls on this criterion, and published mean skull lengths for the two sexes, allocated by this method (Groves 1995b). Considering the great overlap, however, this procedure may not be safe: and the sexual dimorphism did not amount to much in any case. While admitting that there may be some size difference, it seems most realistic to combine all specimens by sex, and reexamine the question later when more material may become available.

Univariate and bivariate analyses

The results of the univariate analyses and bivariate ratios are given in table 1. Skulls from Assam are very much larger than those from elsewhere; those from Southeast Asia (Thailand, Cambodia, Pegu) are slightly smaller than C/U.India in their skull measurements, but their tooththrows are very much shorter.

SP, however, is greatest in Thai/Cambodia, followed by Assam, followed by C/U.India. In 9 out of 26 Assam specimens and 6 out of 11 C/U.India ones, SP is less than twice GSL, but in only a single Thai/Cambodia specimen; on the other hand in 2 from Assam and 3 from Thailand SP is more than 3 times GSL. Thai/Cambodia also have much less inturred horn tips (though not as much as in domestic swamp buffaloes, in which TT is often more than 90% of SP). There is no difference between the three samples in the degree to which the horns reach posteriorly as opposed to laterally: BT as percent of SP averages 61.4 (SD 4.20) in Assam, 59.6 (SD 7.86) in C/U.India and 57.8 (SD 7.37) in Thai/Cambodia.

The Royal Scottish Museum specimen, identified here as the probable type of *Bos arnee* Kerr, falls into the C/U.India range, though at the upper end of it for size: GSL = 581, BB = 243, MT = 158 (272% of GSL), SP = 1130 (194.5% of GSL), TT = 51.9% of SP. None of these values are below the lower limit for the Assam sample (BB nearly is), but on the whole they are much closer to C/U.India.

A specimen from Lagna, southern Vietnam, is difficult to place. GSL is 557, BB = 224, TT = 57.8% of SP, all well within the Thai/Cambodia range, and different from any domestic buffaloes; but MT = 169 (30.3% of GSL), within the range of domestic and Sarawak feral buffalo; SP is only 877 (157.5% of GSL), below any wild buffalo but somewhat large compared to a domestic swamp buffalo. This is the only mainland specimen that might be best interpreted as a wild/domestic hybrid.

Multivariate analyses

The first Discriminant Analysis, using all skull measurements alone (Fig. 1), separates the three samples completely. The Chittagong skull, classed as an unknown for the purposes

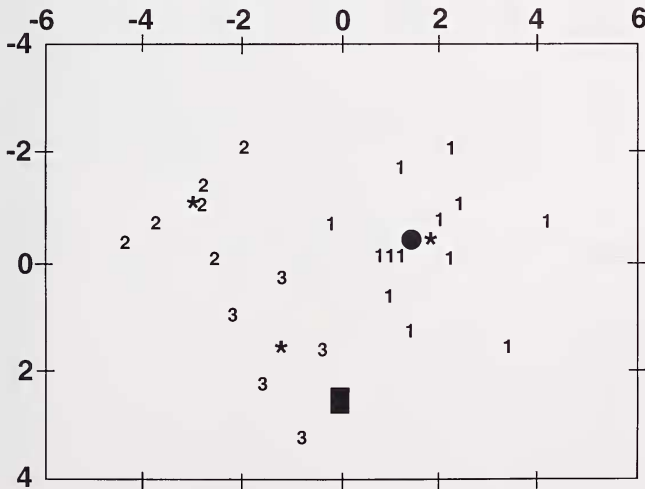


Fig. 1. Discriminant Analysis of 10 skull measurements. First Discriminant Function accounts for 80% of total variance; second, for remaining 17%. 1 = Assam, 2 = C/U.India, 3 = Thai/Cambodia, solid circle = Chittagong, solid rectangle = Lagna, Vietnam. * Group Centroid.

of the analysis, fits well inside the Assam range. The Lagna (Vietnam) skull is closest to the Thai/Cambodia dispersion, but on the edge of it. Inspection of the Discriminant Function coefficients, and the correlations between the Discriminant Functions and original measurements, shows that Function 1 (horizontal) emphasises large size, contrasted with relatively short nasals and narrow posterior part of skull; Function 2 (vertical) contrasts broad skull and long nasals with narrow occiput and width between horn bases.

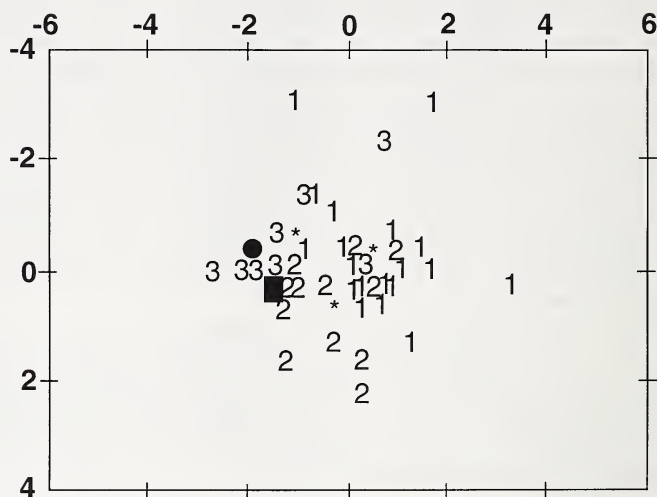


Fig. 2. Discriminant Analysis of 5 horn measurements. First Discriminant Function accounts for 64% of total variance; second, for remaining 36%. 1 = Assam, 2 = C/U.India, 3 = Thai/Cambodia, solid circle = Pegu, solid rectangle = Lagna. Vietnam. * Group Centroid.

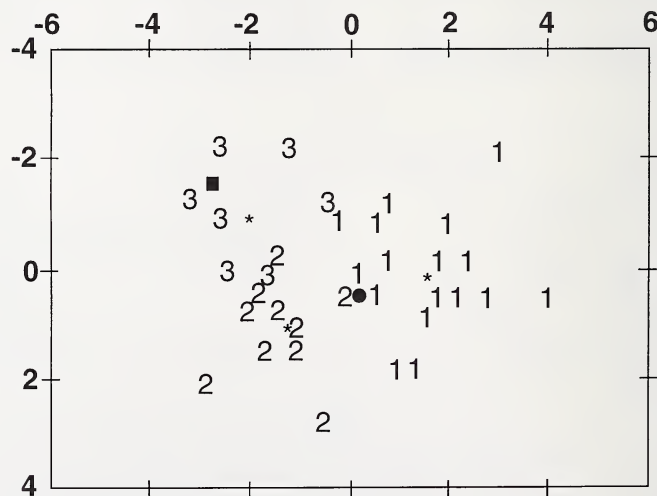


Fig. 3. Discriminant Analysis of 11 skull and horn measurements. First Discriminant Function accounts for 82% of variance; second, for remaining 18%. 1 = Assam, 2 = C/U.India, 3 = Thai/Cambodia, solid circle = presumed type of *Bos arnee* Kerr, solid rectangle = Pegu. * Group Centroid.

The second analysis (Fig. 2), based on all horn measurements, separates the three samples much less clearly; they differ on average only. Function 1 contrasts wide basal diameter and base-to-tip distance with lower tip-to-tip; Function 2 contrasts wide base-to-tip distance with narrow span and base-to-tip distance.

The third analysis (Fig. 3) separates Assam well from the others, but there is a slight overlap between C/U.India and Thai/Cambodia. Function 1 contrasts overall skull size with narrower horn span; Function 2 contrasts wide horn measurements (especially tip-to-tip) with short nasals and narrow postorbital region.

Discussion

Nomenclature

The discriminant analysis based on cranial measurements separates the Assam, C/U.India and Thai/Cambodia samples completely; on this criterion, and on their nearly complete separation in the other two discriminant analyses and their good separation on univariate and bivariate comparisons, they amply qualify as distinct subspecies. Assam buffaloes are distinguished by their very large size; the C/U.Indian form is smaller; and the Thai/Cambodian buffalo, small like the C/U.Indian, has small teeth and exceedingly long horns that turn in less at the tips. A skull from Chittagong fits without difficulty in the Assam sample, and one from Pegu (presumably meaning the Irrawaddy delta) fits in the Thai/Cambodia range. A specimen from Lagna, Vietnam, may be a hybrid between the Thai/Cambodia subspecies and domestic swamp buffaloes.

The first Asian wild buffalo was described by KERR (1792) as *Bos arnee* from a skull in the Edinburgh College Museum and a frontlet and horns from Weir's Museum. He described it as having "long erected semilunar horns... Inhabits India north from Bengal... is of vast size". His figure (No. 746) shows a typical wild buffalo skull. The fate of Weir's Museum is not recorded, but the Royal Scottish Museum, Edinburgh, acquired all the material of the former Edinburgh College Museum (pers. comm. from the late Mr. IAN LISTER), but these specimens are not labelled. I examined several wild buffalo skulls from the old collections, none of known history, in the RSM, and only one of them corresponds to KERR's (1792) figure; its correspondance is in fact very good, both in general appearance despite evident mistakes in the engraving and in its measurements, if KERR's (1792) scale is at all accurate. It is not unlikely that this really is KERR's specimen (Fig. 5). Its measurements, as discussed above, fit best with the Central/Upper India sample, although it verges towards the Assam sample somewhat, and may represent an intergrade population.

The first variant of this same name that I can trace was of BLUMENBACH (1807), who called it "der Riesenbüffel", *Bos arni*, and ascribed it to "den gebirgichten Gegenden von Nord-Hindostan". Given the lack of any more precise indication, this name is most conveniently placed in the synonymy of *arnee*. SMITH (1827) listed *Bos arni* as "the wild buffalo of the Central districts of Bengal" (Shaugur Island and the road to Patna are mentioned), and compared it with the generally domestic, short-horned form, but at the same time distinguishing it from "the Gigantic, or Taurelephant Arnee" from "the upper eastern provinces and forests at the foot of the Himalaya", nearly seven feet high, black, with the tail barely reaching the hocks, and with horns (in a N.Bengal specimen) requiring "the outstretched arms of a man to hold the points"; the Common Arnee he describes as nearly a foot lower at the shoulders, with the tail reaching to near the heels, and the hide more scantily covered with hair. This "Taurelephant Arnee", given the huge size and the distribution, may be the first indication of Assam buffalo.



Fig. 4. Skull of buffalo from Mae Wong, Thailand, NRC unregistered, type of *Bubalus arnee theerapati* new subspecies.



Fig. 5. Skull in Royal Scottish Museum, probably type of *Bos arnee* Kerr.

HODGSON (1841) listed the wild buffalo among the mammals of Nepal, with yet another variant of the name: “*Bubalus arna*, foem. *Arnee*, two varieties. *Macrocerus*, et *Speirocerus*, Nob.H.T. (Habitat Terai)”. HODGSON (1841) appears never to have described his two “varieties”, but GRAY (1852) in the course of cataloguing British Museum skulls, under *Bubalus buffelus*, refers to HODGSON’s forms:

- Two skulls with horns, wild variety. India. Presented by B. H. HODGSON, Esq. *B. B. macrocerus*, Hodgson, l. c., 912.
- Skull, with horns, tame variety. India. Presented by B. H. HODGSON, Esq. *B. B. spirocerus* [sic], Hodgson, l. c., 912.

(The page numbers refer to HODGSON's 1841 study). The museum (now the Natural History Museum) actually has three adult skulls and one immature, as well as two frontlets with horns, presented by HODGSON in 1845. The three adult skulls are 604 k, l and, j (old registrations) = 45.1.8.142, -3 and -4 (current registrations); the first two, male and female respectively, are listed as "wild" by GRAY (1873), the third as "domestic variety". Inferentially, then, the first two would be syntypes of HODGSON's (1841) *macrocerus*, the third the holotype of his *sp[el]irocerus* which, being domestic, is of no further concern to us here. They are presently labelled as being from "Upper India".

GRAY (1852) quotes HODGSON directly, giving no source (perhaps a letter) or date: "In the wilderness, as in the cow-house, there is a marked distinction between the long- (*Macrocerus*) and curve-horned (*Spirocerus*) buffaloes". These characterisation of *macrocerus*, rudimentary though it is, would serve to make the name available; the author and date of the name is thus GRAY, 1852.

Today's Nepalese domestic buffalo is of mixed breed, more Swamp than River type (COCKRILL 1974) though some at least have rather well-curved horns more like a River buffalo (figs. 165, 166); this may be what is meant by the "curve-horned (*Spirocerus*)" variety, although its evident occurrence in the wild, and that of the "long-horned (*Macrocerus*)" variety in a domestic state, is curious. A wild buffalo, captured in Kosi Tappu, in Katmandu Zoo, has wide-spread horns, and Dr JOEL HEINEN (pers. comm.) states that this is usual in the Kosi Tappu buffaloes although there is some variation.

BLANFORD (1891: 492) mentioned HODGSON's (1841) two forms as if they were both wild, describing *macrocerus* as having the horns "almost straight till near the end, where they turn more rapidly upward", and *spirocerus* as "with horns approaching a circle"; and in addition "a very distinct race of a dun colour that inhabits Upper Assam", which he described as *Bos bubalus*, var. *fulvus*. He mentioned "two heads of bulls", in the British Museum and the Indian Museum – from the context, he evidently meant skulls, as he described a convex forehead and short rostrum and nasals. The Indian Museum specimen must be the one from Sadiya (which is in "Upper" Assam, i.e. along the upper reaches of the Brahmaputra in Indian territory), no. 10 in BENTHAM's (1908) list. This is probably an unregistered skull now in the Zoological Survey of India, which has the requisite characters: its measurements correspond approximately to those given by BENTHAM (1908), and it has short nasal bones only (223 mm, nearly all others being above 240 mm). The British Museum (= Natural History Museum, London) skull, however, is readily identifiable: BM 91.8.7.215, a complete skull, was collected in the Mishmi Hills (as far up the Brahmaputra as one can get and still be in India) by Sir G. CAMPBELL and presented to the museum by A. O. HUME in 1891. Stick-on labels give it the Hume Catalogue number 44.A.1, and it has a noticeably convex forehead and short rostrum, including nasals which are 230 mm long. Of these two skulls the more certain identification is the London one, which may be fixed as Lectotype of *fulvus*.

Finally MATSCHIE (1912) described a new subspecies, *Bubalus bubalis* [sic] *septentrionalis*, from "Kuckri-Muckri, N. W. Vorderindien", from a specimen collected by the Crown Prince of the German Reich and of Prussia; Kukri-Mukri (*sic*) is a somewhat isolated island in the Bay of Bengal, off the Sunderbans, the Ganges Delta islands, (Fr. SIGRID RITTHALER, Archivist of the Hohenzollern family, pers. comm.).

All these names, with the exception of *fulvus* Blanford, refer to buffaloes from regions where the "C/U.India" form is known; indeed, in some cases the type specimens themselves have been studied by me, and fall within this form. No names are available for the mainland Southeast Asian wild buffalo, which below is described as new.

GROVES (1994) included a sample of supposedly wild buffaloes from "Bihar" in a preliminary analysis. In retrospect, these are more likely to be domestic (swamp) buffaloes. Even discounting this sample, the hypothesis of derivation of domestic buffaloes from something nearest the present-day Central Indian stock seems quite plausible.

Taxonomy

Three subspecies of the wild buffalo of the Asian mainland may be distinguished, as follows:

Bubalus arnee arnee Kerr, 1792

Synonyms: *arni* Blumenbach, 1807; *macrocerus* Gray, 1852; *septentrionalis* Matschie, 1912.

Distribution: formerly, from the Sunderbans (Ganges delta) southwest into Madhya Pradesh and Andra Pradesh, and northwest into Nepal. Still occurs in the Raipur and Bastar districts of eastern Madhya Pradesh, and the Kosi Tappu reserve, southeastern Nepal.

Diagnosis: a small subspecies, with somewhat larger teeth than others, and horn span less. Greatest skull length generally less than 570 mm, horn span usually less than 1 200 mm., tip-to-tip distance nearly always less than 80% of span. Toothrow length more than 27% of skull length.

Notes: the Panna buffalo (HASAN 1980) was black in colour with contrastingly white lower limbs below the knees and hocks, and a white muzzle. The tail reached about to the hocks. Photos of buffalo from Kosi Tappu, Nepal, in the Katmandu Zoo are very similar.

This subspecies is reduced to tiny remnant stocks, about 100 animals in Kosi Tappu, Nepal (JOEL HEINEN, pers. comm.); and, in 1988, 25 in Uddanti Reserve and 27 spread between Indravati, Bhairamgarh and Pamed Reserves, Madhya Pradesh (H. K. DIVEKAR pers. comm.).

Bubalus arnee fulvus Blanford, 1891

Distribution: Brahmaputra valley, formerly from Kuch Behar to the Mishmi Hills; south to the Chittagong Hills. Still occurs in the Brahmaputra valley from about 92.30 to 96.00 E, and in the Manas district on both sides of the India/Bhutan border (CHOUDHURY 1994).

Diagnosis: a subspecies of very large size, with widely spreading horns whose tips are well turned in. Greatest skull length usually over 570 mm, horn span more than 1 100 mm in most specimens, tip-to-tip distance (as in nominotypical *arnee*) less than 80% of span in almost all specimens. Toothrow length approximately 26–28% of skull length.

Notes: photos of buffalo in Kaziranga and Manas seem to indicate a lighter grey or brownish grey, less blackish, animal than Kosi Tappu specimens or the Panna buffalo, and in particular less contrastingly white on the limbs. Interestingly, given the remarks of SMITH (1827) quoted above, the tail always falls well short of the hocks. Further observations are needed to demonstrate whether these apparent differences hold good over larger series.

A. CHOUDHURY (pers. comm.) estimated the following population numbers for this subspecies in 1992: Manas (Assam and Bhutan), 1 200; Kaziranga and adjacent areas (Assam), 1 100; Laokhowa and adjacent areas (Assam), 200; Laikhimpur (Assam), 100–150; Dibru-Saikhowa and adjacent areas (Assam and Arunchal), 500; Balkharam (Meghalaya), 200; scattered populations in Assam, 29–32; total, 3 300–3 500.

Bubalus arnee theerapati new subspecies

Distribution: formerly from the Irrawaddy delta through Thailand to Cambodia, and probably Vietnam. Now known mainly from Huai Kha Khaeng Wildlife Sanctuary, Thailand; reported from Cambodia.

Type specimen: NRC, Bangkok, unregistered skull, from Mae Wong, Nakhon Sawan, Thailand. (Fig. 4). Judging from its rather slender horns, the specimen may be a female.

Hypodigm: "Koken, E. Siam", 1; Thailand (including "Siam"), 9; Cambodia, 3; Pegu (probably Irrawaddy Delta), 1. Skulls (with horns) only.

Diagnosis: the smallest mainland subspecies on average, with small teeth; horns exceptionally widely spreading, with tips less inturned. Greatest skull length below 570 mm as in nominotypical *arnee*; horn span usually over 1200 mm, tip-to-tip distance more than 80% of span. Toothrow length 24–27% of skull length.

Notes: the only photo I have seen of this subspecies, a distance shot taken by Mr T. PRAYURASUDHI, shows a gray animal, but apparently rather contrastingly marked with white. Photos in LEKAGUL and MCNEELY (1977) were taken in Kaziranga, and do not depict the present subspecies.

The number in Huai Kha Khaeng does not exceed 50 (T. PRAYURASUDHI, pers. comm.). A few still exist in far eastern Cambodia (SUN HEAN, pers. comm.). A pair of wild buffalo horns was found in Yok Don, Vietnam, on the Cambodian border, in 1987 (LE VU KHOI, pers. comm.).

Etymology: the name honours Mr THEERAPAT PRAYURASUDHI (Royal Forestry Department, Thailand), whose continuing fieldwork in Huai Kha Khaeng has added notably to our understanding of the ecology of gaur, banteng and the 50–100 remaining wild buffalo, laying a sound basis for their conservation.

Acknowledgements

Grateful thanks are due to the following curators for allowing access to material in their care, and for assistance in studying it: P. JENKINS, J. CLUTTON-BROCK, L. BARTON, the late IAN LISTER, M. TRANIER, P. BAYLE, H. SCHLIEMANN, R. ANGERMANN, F. W. BRAESTRUP, L. AZZAROLI, L. WERDELIN, the late B. BISWAS, S. CHAKRABORTY and the staff of the Indian Museum, G. U. KURUP, staff of the Indian Forestry College, DEHRA DUN, staff of the National Zoological Reference Collection, Bangkok, J. and R. VAN INGEN, the Maharana of Wankaner, the staff of the Maharaja of Jaipur, and the late Dr. BOONSONG LEKAGUL. Finally I thank my friends and colleagues at the CAMP workshop, Chonburi, July, 1995, at whose behest this study is written; M. K. RANJITSINH for sending me several photos of the Panna buffalo and Ms. Shoshana Greenburg for computing assistance.

Zusammenfassung

Taxonomie des Wasserbüffels (Bubalus arnee) auf dem asiatischen Festland

Schädel und Hörner des Wasserbüffels (*Bubalus arnee*) aus Indien und Südostasien wurden morphometrisch untersucht. Trotz einer hohen individuellen Variationsbreite konnten drei Unterarten unterschieden werden. Eine davon, die Population in Thailand und Kambodscha umfassend, wurde in der vorliegenden Arbeit neu beschrieben. Aus dem Verlust oder der Fehlzuordnung von Typusexemplaren resultierende nomenklatorische Probleme wurden geklärt.

References

- ARUN SINGH, T. (1980): Feedback: "The enigmatic buffalo". *Hornbill* **1980**, 4.
 BENTHAM, T. (1908): An illustrated Catalogue of the Asiatic Horns and Antlers in the Collection of the Indian Museum. Calcutta: Indian Museum.
 BLANFORD, W. T. (1891): Fauna of British India. London: Taylor and Francis.
 BLUMENBACH, J. F. (1807): Handbuch der Naturgeschichte. 8th ed. Göttingen: Heinrich Dieterich.
 CHOUDHURY, A. (1994): The decline of the wild water buffalo in north-east India. *Oryx* **28**, 70–73.
 COCKRILL, W. R. (1974): The Husbandry and Health of the Domestic Buffalo. Rome: Food and Agriculture Organization of the United Nations.
 GRAY, J. E. (1852): Catalogue of Mammalia. Vol. **3**, Ungulata. London: British Museum Trustees.
 GRAY, J. E. (1873): Handlist of the Edentata, Thick-skinned and Ruminant Mammals in the British Museum. London: British Museum Trustees.

- GROVES, C. P. (1969): Systematics of the Anoa (Mammalia, Bovidae). *Beaufortia* (Amsterdam) **17**, 1–12.
- GROVES, C. P. (1995 a): On the nomenclature of domestic animals. *Bull. Zool. Nomencl.* **52**, 137–141.
- GROVES, C. P. (1995 b): Domesticated and commensal mammals of Austronesia and their histories. In: *The Austronesians: Historical and Comparative Perspectives*. Ed. by P. BELLWOOD, J. J. Fox, and D. TRYON. Canberra: Research School of Pacific and Asian Studies, Australian National University. Pp. 152–163.
- HASAN, S. M. (1980): The enigmatic buffalo. *Hornbill* **1980**, 26–27.
- HEDGES, S. (1995): Asian Wild Cattle and Buffaloes: Status Report and Conservation Action Plan. 2 vols. WWF Project 3950/Asia.
- HERRE, W.; RÖHRS, M. (1990): *Haustiere – zoologisch gesehen*. 2. Aufl. Stuttgart, New York: Gustav Fischer.
- HODGSON, B. H. (1841): Classified catalogue of Mammals of Nepal (corrected to end of 1841, first printed in 1832). *J. Asiat. Soc. Bengal* **10**, 907–916.
- KERR, R. (1792): The Animal Kingdom of the celebrated Sir Charles Linnaeus. Class I. Mammalia. London: J. Murray.
- LEKAGUL, B.; MCNEELY, J. A. (1977): Mammals of Thailand. Bangkok: Assoc. Conservation of Wildlife.
- LINNAEUS, C. (1758): *Systema Naturae per Regna Tria Naturae, secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis*. I: Regnum Animale. 10th ed. Holm: Laurentius Salvius.
- MATSCHE, P. (1912): Beutestücke aus fernen Ländern. *Dt. Jäger-Zeitung* **59**, 97–103.
- SMITH, C. H. (1827): Vol. 4 of GRIFFITH.: E. The Animal Kingdom, arranged in conformity with its organisation by the Baron Cuvier. London: Geo. B. Whittaker.
- THOMAS, O. (1911): The Mammals of the Tenth Edition of Linnaeus; an Attempt to fix the Types of the Genera and the exact Bases and Localities of the Species. *Proc. Zool. Soc. Lond* **1911**, 120–158.

Author's address: COLIN P. GROVES, Department of Archaeology and Anthropology, Australian National University, Canberra, A. C. T. 0200, Australia.